HISTORICAL PERSPECTIVES OF ANGIOSPERM EVOLUTION

Symposium volumes represent temporal nodes that lend themselves to taking stock of various disciplines. In the case of angiosperm paleobotany, the last major symposium volume, "Origin and Early Evolution in Angiosperms," C. B. Beck (editor), appeared eight years ago. Although that particular volume (Beck, 1976) stressed origin and early evolution only, some appreciation of changes in emphasis and approach in angiosperm paleobotany since that time may be gained by considering this volume in the perspective of its predecessor.

Historically, angiosperm paleobotany turned a corner 15–20 years ago. And in some ways, several papers published since that time represent a quantum change in the character of the field that brought angiosperm paleobotany in line with modern paleontological investigations. Previously, floristic investigations were emphasized and attention to individual fossils, their morphological characters and critical assessments of their affinities were secondary. As a result, generally, studies of relatively Recent (Neogene) floras had much validity while the identifications based on superficial features made many conclusions based on studies of older fossils erroneous (Dilcher, 1974). In addition, little was contributed to our understanding of evolution within the angiosperms. The confusion resulting from such approaches is well known.

As problems became evident in older paleobotanical research, the direction in angiosperm studies shifted to a more careful approach emphasizing the evaluation of the fossils themselves and the establishment of their affinities. This largely empirical direction was an important element in angiosperm paleobotany for a long time. Perhaps the excesses of previous researchers induced the response of willful myopia in many scientists during this conservative phase of angiosperm paleobotany. Whatever the motivating factors, it is only 15 to 20 years since the beginning of the trend in angiosperm paleobotany in which the investigation of evolution has been based upon newly devised systematic techniques and the recognition of extinct angiosperm forms, as well as patterns in the fossil record.

The present collection of papers provides an opportunity to gain some overview of the contemporary field of angiosperm paleobotany and, thus, to see how emphases have changed. While these manuscripts do not illustrate all that has been done recently in angiosperm paleobotany, they provide a representation of current work in this field. It is now possible to observe that certain areas of emphasis that were gathering momentum ten years ago have continued to become increasingly important, while other entirely new areas of concentration have become significant.

These following papers, as contributions to an international symposium on angiosperm paleobotany, represent a broad spectrum of research in both subject and philosophy. It would certainly serve our immediate purposes if all of them could be nested neatly under the rubric of modern angiosperm paleobotany and if each illustrated some extension of a commonly held philosophy. Yet the fact that this cannot be easily done is quite informative. There remain differences in approach in the modern scientific community studying angiosperm paleobotany, and there remain significant differences in attitude. These extend at times even to varying interpretations of particular fossil organs. Certainly, with respect to modern angiosperm paleobotany, V. Krassilov is an iconoclast whose contribution to this volume reveals more than his attitude. Krassilov's paper makes it clear that there are certain enigmatic early angiosperm fossils that need further investigation and that there is still disagreement as to the interpretation of angiosperm ancestry within the paleobotanical community. The contribution by Hughes also stands somewhat apart because he takes an overview pointing to some of the nagging problems in Mesozoic angiosperm paleobotany and makes some innovative proposals to deal with them.

The other papers are easier to group and illustrate where the field has been going during the past few years. Perhaps most obvious is the continuity in studies of angiosperm pollen. Doyle (1969), Muller (1970), and Brenner (1963, 1967) had (and continue to have) important impact during the late 1960s and early 1970s. Doyle's contribution was noteworthy because it stressed pattern in the context of evolution while Brenner stressed evolutionary history in the context of paleobiogeography, and Muller emphasized the importance of the critical evaluation in palynology to reveal past record of extant flowering plants.

Studies of palynology continue to stress pattern and history, but, in this volume, micromorphology and ultrastructural analysis are also important. Walker and Walker illustrate how careful analysis of single Lower Cretaceous palynomorphs can contribute to our understanding of variation in early angiosperm pollen, variation that might be misleading or go unnoticed without the application of modern techniques, and point out similarities between certain well-known Cretaceous palynomorphs and pollen of modern taxa. Zavada concentrates on morphological analysis of monosulcate pollen by proposing evolutionary trends based on modern taxa and carefully evaluating taxonomic characters used to distinguish angiosperm pollen from gymnosperm pollen. He then examines certain fossil palynomorphs, often pre-Cretaceous, in the context of their possible significance to angiosperm origins. Muller summarizes angiosperm history based on the palynological record and notes significant events in angiosperm evolution and evolutionary patterns. Muller's selective approach to the palynological literature, based on careful morphological analysis, gives credibility to the utility of the dispersed pollen record in documenting angiosperm history.

A relatively new area of angiosperm research involving the study of flowers and inflorescences has become a significant part of angiosperm paleobotany. Since serious investigations of fossil flowers and inflorescences have begun (e.g., Crepet et al., 1974, 1975; Tiffney, 1977), such investigations have become more common and have been conducted at various levels. Further evidence of their continuing importance are four papers reporting new floral finds by Dilcher and Crane, Crane and Dilcher, and Schaarschmidt and Friis. Fossil floral remains have also been used in the paper by Crepet to assess the importance and success of faithful pollinators in flowering plant history.

Another important and interesting aspect of angiosperm paleobotany involves emphasis on fruits. Bruce Tiffney's contribution to this symposium volume incorporates fruit and seed data in an analysis of the history and significance of animal dispersal of angiosperm fruits. Crepet and Tiffney's contributions both emphasize plant-animal interactions in an effort to assess the significance of animal involvement in angiosperm radiation and speciation from fossil data. Dilcher and Crane and Crane and Dilcher combine analyses of both fruiting material and flower forms, demonstrating that some early angiosperms shared the characteristic features and apparent reproductive biology of the Magnoliidae. Several associated plant organs are assumed to represent a single taxon based upon stratigraphy and anatomy in an effort to reconstruct a whole flowering and fruiting shoot of an ancient angiosperm. The flowering shoot has features which indicate that the co-adaptive evolution between floral morphology and pollinators was important by the mid-Cretaceous.

Leaf studies have been extremely important and recent emphases on fine venation analysis and cuticular features of fossil leaves have proven essential in interpreting their affinities (Hickey, 1973; Dilcher, 1974). The significance of pollen and leaf remains from the Atlantic Coastal Plain are well known (Hickey & Doyle, 1977), and Upchurch has analyzed patterns in the evolution of the cuticular features of angiosperm leaves from these deposits.

Emphasis on pattern with an eye on evolution in an ecological context continues to be important in angiosperm paleobotany. Such emphasis transcends the analysis of any one particular type of organ. However, sources of data once thought beyond the scope of angiosperm paleobotany (e.g., leaf cuticles, pollen ultrastructure, and floral structure) are proving valuable sources of insight into different aspects of angiosperm history that will prove important in understanding their evolution. In addition, it is obvious that morphological analysis has become extremely important in angiosperm paleobotany giving credibility to the assessment of relationships between fossil and modern taxa, providing a better idea of past variation, and potentially allowing a better assessment of homologies.

From the paleobotanical work represented here it is possible to speculate on the areas of important directions in angiosperm paleobotany. First, pattern analysis has the potential for contributing to our understanding of the process of evolution and to the understanding of certain evolutionary events in the context of ecology. Second, increasingly sophisticated morphological analysis, character state analysis, and knowledge of variability in extant as well as related extinct taxa combined with increasingly sophisticated systematic methods have great potential for having fossil angiosperm data make an important contribution to the classification of the flowering plants. Finally, it should be evident that empirical contributions (i.e., studies of fossils, their affinities, analysis of their characters in the context of related modern taxa including the establishment of homologies) will continue to be an important aspect of angiosperm paleobotany.

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